STORM-INDUCED COMMUNITY DYNAMICS IN THE FEZOUATA BIOTA (LOWER ORDOVICIAN, MOROCCO)

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ABSTRACT

In the Central Anti-Atlas (Morocco), the lower part of the Fezouata Shale has yielded locally abundant remains of soft-bodied to lightly-sclerotized taxa, occurring in low diversity assemblages characterized by strong spatial and taxonomic heterogeneities, and frequently, by the occurrence of small-sized individuals. Size frequency analyses of *Celdobolus* sp., *Wosekella* sp. (both linguliformean brachiopods) and *Babinka prima* (babinkid bivalve) collected in deposits of the Fezouata Shale and associated with distinct paleoenvironmental conditions show that short-lived communities of epifaunal and shallow infaunal taxa were regularly smothered and killed by distal storm deposits. Small-sized individuals more likely represent juveniles, rather than 'dwarfed' adults (Lilliput

Effect). Consequently, unstable environmental conditions (regular storms, and possibly low oxygenation of the water column) probably explain the unusual community dynamics of late Tremadocian assemblages of the Fezouata Biota (high density of individuals, low α-diversity, and high γ-diversity), interpreted as short-lived, opportunistic populations. This process has wider implications for the understanding of occurrences of small individuals elsewhere in the fossil record.

INTRODUCTION

Discovered in the early 2000s in the Central Anti-Atlas of Morocco, the Early Ordovician Fezouata *Lagerstätte* has dramatically altered evolutionary scenarios on the initial diversification of metazoans during the Early Paleozoic (Van Roy et al. 2010, 2015a; Lefebvre et al. 2016a; Martin et al. 2016a). In the Zagora area, the ~900 meter thick siltstones of the Fezouata Shale (Fig. 1A) have yielded over 200 taxa of marine invertebrates, the majority of which are shelly organisms typical of the Great Ordovician Biodiversification Event including asterozoans, bivalves, rhynchonelliformean brachiopods, cephalopods, crinoids, gastropods, graptolites, ostracods, trilobites (Havlíček 1971; Destombes et al. 1985; Ebbestad 2016; Gutiérrez-Marco and Martin 2016; Lefebvre et al. 2016b; Martin et al. 2016b; Polechová 2016). The Fezouata Biota also comprises a high number of soft-bodied to lightly sclerotized taxa, generally preserved as colorful iron oxides, resulting from the weathering of pyrite (Van Roy 2006; Van Roy et al. 2010, 2015a; Lefebvre et al. 2016a; Martin et al. 2016a). Some of these exceptionally preserved organisms (e.g., cirripede crustaceans, eurypterid and xiphosuran chelicerates) represent the oldest occurrences of particular marine invertebrates, previously recorded from younger Paleozoic *Lagerstätten* (Van Roy et al. 2010, 2015a). However, the Fezouata Biota also includes numerous representatives of soft-bodied to lightly sclerotized groups typical of early–middle Cambrian, Burgess Shale-type *Lagerstätten* (e.g.,

anomalocaridids, protomonaxonids, armoured lobopodians, marrellomorphs, naraoiids; Botting 2007, 2016; Van Roy et al. 2010, 2015b; Van Roy and Briggs 2011; Legg 2016).

During the Early Ordovician, the Central Anti-Atlas was located at high latitudes close to the paleo-South pole (Fig. 1D; see Torsvik and Cocks 2011, 2013). In the Zagora area, the Fezouata Shale was interpreted to have been deposited in a storm-wave dominated, cold-water, shallow environment, indirectly influenced by tides (Martin et al. 2016a; Vaucher et al. 2016, 2017). The corresponding paleoenvironment ranges from the shoreface (*sensu* Reading 1996) to the upper offshore, i.e. close below the storm wave base (Vaucher et al. 2017). In the Fezouata Shale, the distribution of exceptionally preserved fossils (EPF) is not random, but associated with a narrow window of favourable environmental conditions, around the storm-wave base (Martin et al. 2016a; Vaucher et al. 2016, 2017). EPF-bearing levels typically occur as lenses, located immediately below thin (mm to cm) levels of coarser siltstones to sandstones (Martin et al. 2015; Vaucher et al. 2016). The Fezouata Biota was thus interpreted as *in situ* assemblages, smothered by distal storm deposits (Lefebvre et al. 2016a; Martin et al. 2016a; Vaucher et al. 2016, 2017).

In the Lower Ordovician succession of the Zagora area, favourable environmental conditions for exceptional preservation are located at two distinct stratigraphic intervals (Fig. 1A; Lefebvre et al. 2016a, 2018; Martin et al. 2016a). Based on acritarchs, conodonts, and graptolites (Gutiérrez-Marco and Martin 2016; Lefebvre et al. 2016a, 2018; Lehnert et al. 2016; Martin et al. 2016a; Nowak et al. 2016) a late Tremadocian age (Tr3) was proposed for the lower, about 70 m thick interval. The upper EPF-bearing interval is narrower (~50 m thick), and it occurs about 240 m higher in the succession (Lefebvre et al. 2016a, 2018). Graptolites suggest a mid Floian age (Fl2) for this upper interval (Gutiérrez-Marco and Martin 2016; Lefebvre et al. 2016a, 2018).

Community structures are markedly different in the two EPF-bearing intervals (Lefebvre et al. 2018). In the Zagora area, all fossiliferous horizons sampled in the upper interval have yielded comparable, particularly abundant and diverse fossil assemblages (~50 taxa), dominated by bivalves, rhynchonelliformean brachiopods, cephalopods, gastropods, and trilobites (Destombes et al. 1985; Vidal 1998; Kröger and Lefebvre 2012; Ebbestad 2016; Polechová 2016). Exceptionally preserved taxa are rare and constitute a minor component of the fauna (Van Roy 2006; Van Roy and Tetlie 2006; Botting 2016; Lefebvre et al. 2016a, 2018; Ortega-Hernández et al. 2016). In contrast, EPF are particularly abundant and diverse in the lower interval. Both EPF and shelly fossils occur massively in thin, discontinuous levels, yielding low diversity assemblages generally dominated by one or two taxa, e.g., anomalocaridids, linguliformean brachiopods, conulariids, cornute stylophorans, eocrinoids, graptolites, hyolithids, marrellomorphs, sponges, trilobites, and/or xyphosurans (Botting 2007, 2016; Van Roy et al. 2010, 2015a, 2015b; Van Roy and Briggs 2011; Martin et al. 2015; Gutiérrez-Marco and Martin 2016; Lefebvre et al. 2016b; Van Iten et al. 2016; Allaire et al. 2017). In this interval, each individual horizon has yielded a unique assemblage, in terms of faunal content and/or relative proportions of occurring taxa. One of the most striking features of fossil assemblages recovered from the lower EPF-bearing interval is thus their extreme taxonomic and spatial heterogeneity (Van Roy et al. 2015a; Botting 2016; Lefebvre et al. 2016b). The high cumulative diversity (γ-diversity) recorded in this interval (~150 taxa) suggests that the low diversity observed for each individual assemblage (α-diversity) could represent a kind of random sampling of a larger pool of taxa.

Another intriguing feature reported from several upper Tremadocian horizons yielding EPF in the Zagora area is the repeated occurrence of taxa represented exclusively by small-sized individuals: this phenomenon has been described in eocrinoid and stylophoran echinoderms (Lefebvre and Botting 2007; Lefebvre et al. 2016b), gastropods (Ebbestad 2016), and trilobites

100 (Martin 2016). In both echinoderms and gastropods, it is difficult to identify, whether such
101 assemblages of small-sized individuals are comprised of only juveniles, or if they correspond
102 to populations of 'dwarfed' adults (Lefebvre and Botting 2007; Ebbestad 2016; Lefebvre et al.
103 2016b). On the other hand, the assemblage of small-sized trilobites (*Anacheirurus adserai* and
104 *Bavarilla zemmourensis*) reported by Martin (2016) is apparently composed of meraspid (adult)
105 individuals, about half their 'standard' size documented in other levels and/or geographic areas.
106 The study of body size is important to understand the biological and ecological adaptations
107 of an individual to its environment (Jablonski 1996; Vermeij 2016). Previous studies have
108 explained spatial differences in body sizes in marine settings, either by post-mortem processes
109 (e.g., fossil sorting and preservation; Brenchley and Harper 1998) or by the pre-mortem
110 chemical conditions of the water column and sediments. These conditions reflect mainly
111 oxygen fluctuations (Savrda and Bottjer 1986; Payne and Clapham 2012; He et al. 2017) and
112 nutrient availability (Twitchett 2007; He et al. 2010). Consequently, the aim of this paper is to
113 identify the physical mechanisms (e.g., storm influence) possibly involved in body-size changes
114 in late Tremadocian fossil assemblages of the Fezouata Shale. This study is focused on
115 brachiopods and bivalves, which constitute a key element of benthic communities in the
116 Fezouata Biota (Havlíček 1971; Mergl 1981; Babin and Destombes 1990; Destombes et al.
117 1985; Van Roy et al. 2010, 2015a; Polechová 2016), and the diversification of which was a
118 major component of the Great Ordovician Biodiversification Event (Harper 2006; Servais and
119 Harper 2018). The size distribution of three benthic taxa (the bivalve *Babinka* and the two
120 brachiopods *Celdobolus* and *Wosekella*) is analysed, because they are relatively abundant, well
121 preserved, easily identifiable and all occur at various horizons spanning a wide range of
122 environmental conditions in the late Tremadocian EPF-bearing interval of the Zagora area.
123
124 MATERIAL AND METHODS

Over 300 specimens of bivalves and brachiopods were collected from seven different localities in the lower interval yielding EPF (*Araneograptus murrayi* graptolite Zone, late Tremadocian) in the Fezouata Shale. The position of these localities along a proximal-distal axis and in the Zagora area is shown in Fig. 1B and Fig. 1C respectively. For this study, only specimens belonging to the three genera *Celdobolus*, *Wosekella* and *Babinka* were included (Fig. 2), because these three taxa are suitably abundant at all sites. This choice was further motivated by the putative modes of life of these three taxa. *Celdobolus* has been interpreted as a typical epifaunal genus, possibly epizoic on sponges (Mergl 2002). Cambrian species of *Wosekella* have been interpreted in some occurrences as semi-infaunal low suspension feeders (Mergl and Kordule 2008) or epifaunal (attached with the pedicle to the substrate; see Pettersson Stolk et al. 2010). However, Ordovician *Wosekella* is generally interpreted as endobenthic (Mergl 2002). *Babinka*, a primitive bivalve, is regarded as a shallow-water infaunal taxon (Guild G5 suspensivorous – free endofaunal of Sánchez 2008; see also McAlester 1965; Polechová 2016), based on the subcircular outline and globose profile of the shell. For measurements and analyses, only complete shells were retained. The width W, the length L, and the height H of different shells were measured using a Zeiss SteREO Discovery.V8 stereomicrocope linked to a Zeiss AxioCam MRc5 digital camera with a precision of 0.01 mm. The body size G=(L+W)/2 (Fig. 3) was calculated for brachiopods according to Jablonski (1996), and for bivalves: G=(H+L)/2 (Fig. 3) according to Carter et al. (2012). Afterward, the mean size for each genus was determined. Data were plotted as size-frequency histograms in PAST. Then Shapiro-Wilk test for normality was made. For normal distributions, a Student t-test was applied to check if there is a significant difference in size between sites (Hammer et al. 2001).

All studied material is registered in the collections of the Cadi Ayyad University, Marrakesh (Morocco). Precise GPS coordinates of the studied localities are reported on specimen labels, and are available upon request.

RESULTS

The studied specimens consist of disarticulated valves that do not show any preferential orientation (simply disarticulated by wave orbitals, with no or limited transport before burial; Vaucher et al., 2016, 2017). The majority of sampled valves were complete, without any evidence of damage or abrasion. They were preserved at the base of storm events (covered by fine sandstones or coarse siltstones showing normal grading or oscillatory structures; Vaucher et al. 2016, 2017).

Both *Celdobolus* and *Babinka* show normal distributions at all sites (Fig. 3A, B) with an increase in size from proximal to distal localities (Fig. 3A). The difference in body size between sites is significant (Fig. 3C). *Wosekella* has a normal distribution at all localities (Fig. 3A, B). However, no trend can be observed from shallow to deeper environments (Fig. 3A). In addition to that, the size differences between sites is not significant (Fig. 3C).

DISCUSSION

The mean size values observed for *Wosekella* at all sites are comparable to those reported for this genus in Lower Ordovician deposits from other regions (e.g., Bohemia; Mergl 2002). Similarly, the mean size values obtained for both *Babinka* and *Celdobolus* in the distal-most site are similar to those described for this genus in other areas (e.g.; Bohemia; McAlester 1965; Mergl 2002; Polechová 2013). In marked contrast, specimens of both *Babinka* and *Celdobolus* from Z-F50 are about half the size of those occurring in both Z-F4 and other Early Ordovician assemblages (McAlester 1965; Mergl 2002; Polechová 2013). This significant difference in the mean size of *Babinka* and *Celdobolus* from the Fezouata Shale can be explained either by post-mortem or pre-mortem processes.

Post-mortem taphonomic processes include fossil sorting and preservation (Kidwell 1991; Brenchley and Harper 1998). At all sites, brachiopods and bivalves are apparently preserved *in situ* with little to no evidence of significant lateral transport (disarticulated but complete valves with no preferential orientation) (Vaucher et al. 2016, 2017), and even minute details of the shells, such as setae in siphonotretoid brachiopods, are often perfectly preserved. The preservation of such extremely delicate and brittle structures rather suggests the *in situ* burial of autochthonous benthic populations by distal storm deposits. Thus, the abundance of small-sized assemblages of bivalves and *Celdobolus* in proximal sites cannot simply be interpreted as resulting from sorting and preservation.

During pre-mortem processes, chemical parameters (e.g., low oxygen concentrations, oligotrophic waters) have been frequently invoked to explain severe reductions in the mean size of adults in populations of marine invertebrates (Tasch 1953; Urlichs 2012; Botting et al. 2013). This phenomenon ('Lilliput Effect') has been advocated for marine faunas, particularly those associated with the survival and recovery phases following extinction events (e.g., Huang et al. 2010; Twitchett 2007). The Lilliput Effect generally affects most elements of the biota, across a wide range of taxonomic levels. In the Fezouata Shale, the possible occurrence of a Lilliput Effect was questioned for several low-diversity assemblages from the lower EPF-bearing interval, yielding small-sized trilobites (Martin 2016), echinoderms (Lefebvre et al. 2016b), and gastropods (Ebbestad 2016). At proximal sites, however, there is no evidence supporting the existence of a putative Lilliput Effect: with the exception of *Babinka*, *Celdobolus* and possibly some other co-occurring epibenthic brachiopod genera (*Elliptoglossa*, *Monobolina*, and *Orbithele*), all other components of the associated benthic fauna (including trilobites and some brachiopods, such as *Wosekella*; Fig. 2A) do not show any reduction in size. Unfavorable chemical conditions should have affected the whole benthos. In these sites, small-sized specimens of *Babinka* thus more likely correspond to juveniles, rather than to 'dwarfed' adults.

198 Physical parameters of the water column (e.g., storm intensity, currents) are other pre-
199 mortem processes possibly involved in the observed pattern of size distribution. When
200 entombed by sediment, deep infaunal organisms have a greater chance of physically being able
201 to react than epifaunal or shallow infaunal ones (Freeman et al. 2013). Taxa like *Wosekella* with
202 a reduced dorsal pseudointerarea and smooth, elongate suboval valves (Emig 1997; Bassett et
203 al. 1999) have the capability to re-orient upward and the possibility of burrowing upwards.
204 Hammond (1983) described that in experimental conditions, 100% of *Lingula anatina* buried
205 in 5 to 10 cm of sediment survived, and 70% of *L. anatina* with pedicles emerged from 20 cm
206 of sediment. Moreover, Thayer and Steele-Petrovic (1975) demonstrated that, using modern
207 genus *Glottidia*, after entombment, reorientation and re-burrowing were successful, even in the
208 case of animals losing their pedicles. On the other hand, Hutchinson et al. (2016) showed a high
209 mortality of sessile epibenthic bivalves after their burial by sediment. As it is the case during
210 storms, even shallow infaunal taxa are subjected to the power of the wave orbitals, which
211 snatches the animals from their life position in the burrow. The result is that the organisms may
212 become disoriented and lie in a position that is far from their normal life position.
213 In the Fezouata Shale, the storm record varies between localities and between different levels
214 at the same locality (Vaucher et al. 2017). During storm events, wave orbitals generated in the
215 water column, in addition to the quantity of burial material, if any, clearly had an impact on
216 benthic communities. Proximal, shallow-water settings were more affected by storms and wave
217 orbitals, and larger amounts of sediment were deposited than in more distal, deeper-water
218 environments (Vaucher et al. 2016, 2017). In this context, the demographics observed for
219 *Babinka, Celdobolus* and *Wosekella* in the Fezouata Shale can be simply explained by both
220 their presumed mode of life and physical ability to re-burrow and reorient to their normal life
221 orientation, and external physical parameters (e.g., storm intensity) depending on their position
222 along a proximal-distal gradient. In proximal settings (e.g., Z-F50), shallow infaunal taxa (e.g.,

223 *Babinka*) are exclusively represented by small-sized, probably juvenile individuals, whereas
224 deeper infaunal genera that actively respond to physical stress exhibit a much wider range of
225 sizes, including putative adult individuals. This suggests that, in shallow-water settings,
226 populations of *Babinka* were regularly smothered and killed by thin, distal storm deposits, thus
227 preventing the development of stable communities on the sea floor. In contrast, individuals of
228 *Wosekella* were less affected and could reach larger sizes. In more distal environments (e.g., Z-
229 F4), both epibenthic/shallow infaunal *(*e.g. *Babinka, Celdobolus)* and deep infaunal (e.g.
230 *Wosekella)* communities were little affected by storms, so that individuals could reach larger
231 sizes and form stable, ageing populations (Fig. 4). Consequently, in the lower EPF-bearing
232 interval of the Fezouata Shale, reaching large sizes in an environment constantly affected by
233 storms seems to be related to a better luck when colonizing the sea floor, due to larval transport
234 by fair weather currents. These currents allowed randomly the (re)colonization of either a high
235 or a low-energy setting, thus permitting or preventing the growth of *Babinka, Celdobolus* and
236 possibly other epibenthic or shallow infaunal taxa into full-sized adults.
237 In the late Tremadocian of the Zagora area, the persistence of unstable environmental
238 conditions in shallow settings prevented the colonisation of the sea bottom by stable, long-
239 ranging communities of sessile or slow-moving epibenthic/shallow infaunal taxa. These
240 stressful environmental conditions probably explain the high spatial and taxonomic
241 heterogeneity observed in this interval of the Fezouata Shale, and support the interpretation of
242 the low-diversity assemblages occurring in these levels as opportunistic populations buried *in*
243 *situ* by distal storm deposits. This interpretation is in good agreement with previous reports of
244 similar, low diversity, Early–Mid Ordovician benthic assemblages dominated by primitive
245 bivalves (Cope 1999; Sánchez and Benedetto 2007) and/or by linguliformean brachiopods
246 (Popov et al. 2013).
247

CONCLUSIONS

The low-diversity, dense assemblages occurring in most fossiliferous horizons of the late Tremadocian EPF-bearing interval of the Fezouata Shale are not generated by currents, but they correspond to autochthonous communities smothered by distal storm deposits (Martin et al. 2015, 2016a; Vaucher et al. 2016, 2017). Both the spatial heterogeneity and unusual demographics displayed by these assemblages can be explained by relatively unstable environmental conditions, both in terms of oxygenation (dysoxic to anoxic settings; see Botting 2016; Martin et al. 2016b) and storm activity (Vaucher et al. 2016). It is thus very likely that the particularly dense and patchy, low diversity assemblages observed in this interval correspond to successive colonizations of the sea floor by opportunistic taxa (Botting 2016; Lefebvre et al. 2016b). At several horizons, the small size of most individuals suggests that these epibenthic or shallow infaunal populations were short-lived and repeatedly buried by distal storm deposits.

This study also constitutes the first step to elaborate a proxy, at generic level, relating shell sizes to bathymetry, in a storm-wave dominated environment. Additionally, it shows that a new mechanism, related to physical processes, can explain size differences independently from the chemical conditions of the water column and their related dwarfism. Finally, this study highlights the utility of understanding life habit and more broadly paleoecology for fully understanding fossil assemblages.

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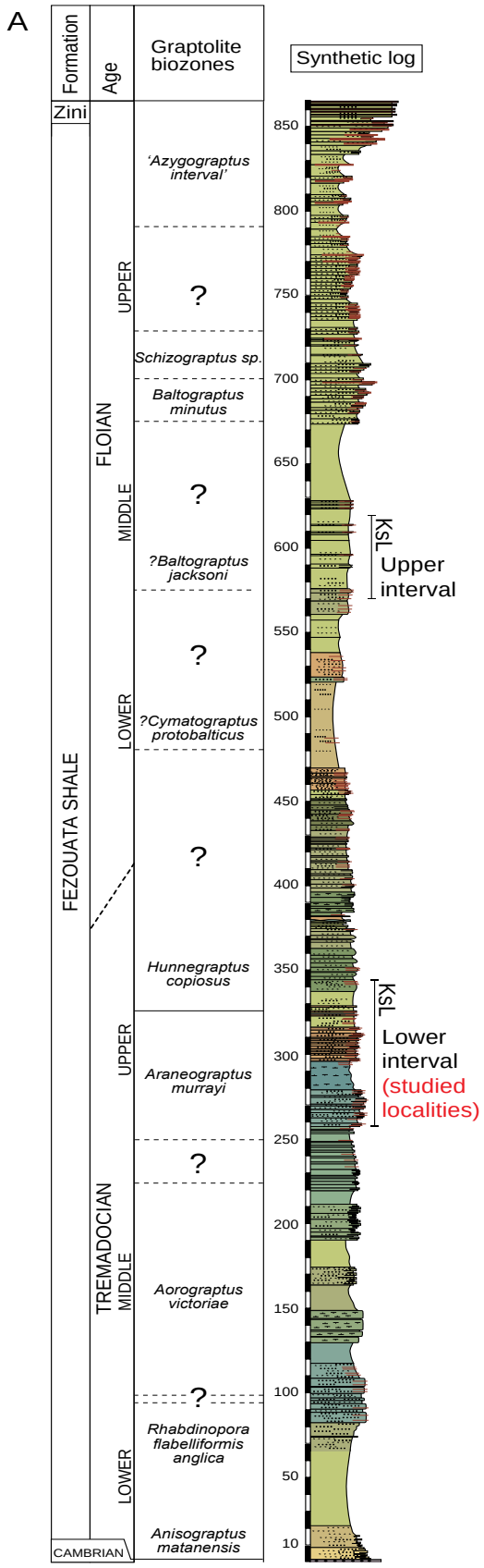
FIGURE CAPTIONS

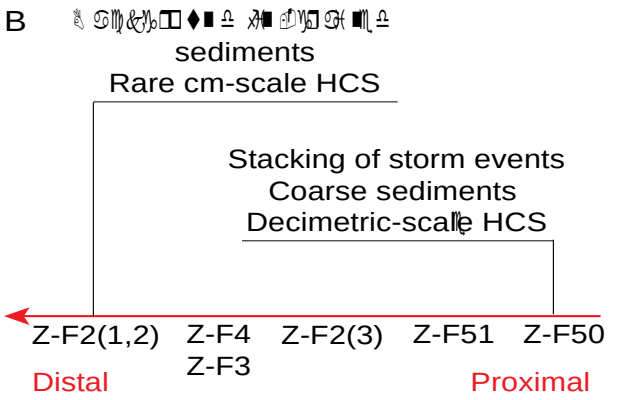
FIG. 1.—Geologic context of the studied material. **A)** Synthetic stratigraphic column of the Lower Ordovician succession in the Zagora area, Morocco showing the position of the two intervals yielding exceptionally-preserved faunas (KsL); modified from Gutiérrez-Marco and Martin (2016) and Lefebvre et al. (2018). Colors on the log correspond to those of the rocks exposed. **B)** The position of studied levels along a proximal-distal axis. **C)** The position of studied localities in the Zagora region. **D)** The Early Ordovician and current position of the Zagora area.

FIG. 2.—Late Tremadocian babinkid bivalves and linguliformean brachiopods from the Fezouata Shale, hill east of Tamegroute, Zagora area, Central Anti-Atlas (Morocco). **A–B)** *Babinka prima* Barrande, 1881; scale bars: 2 mm. **A)** AA-TGR1c-OI-178. **B)** AA-TGR1c-OI-14. **C–D)** *Wosekella* sp.; scale bars: 2 mm. **C)** AA-TGR1c-OI-102. D) AATGR1c-OI-155. **E–F)** *Celdobolus* sp.; scale bars: 2 mm. **E)** AA-TGR1c-OI-78. **F)** AA-TGR1c-OI-62.

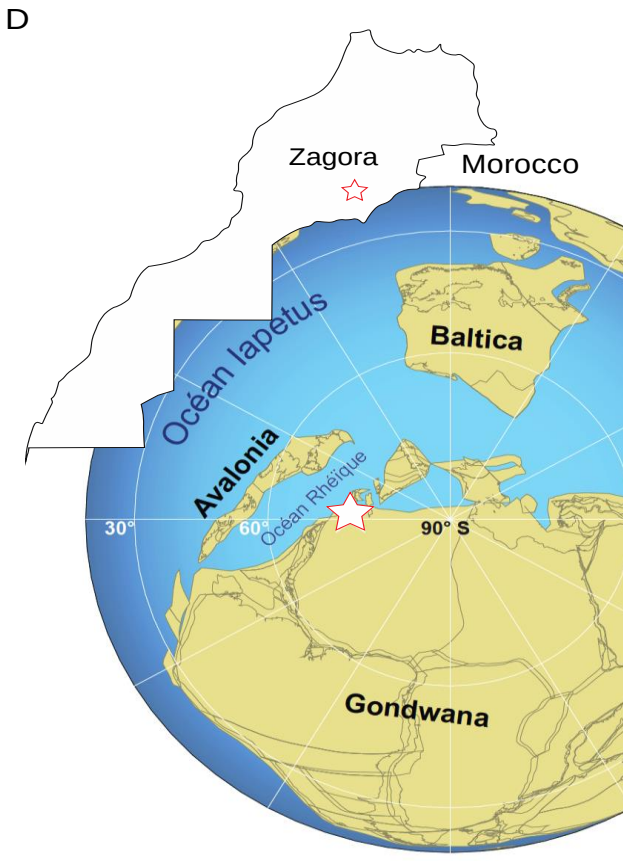
FIG. 3.— Statistical analysis on brachiopods and bivalves in the Fezouata Shale, Zagora area (Morocco). **A)** Size distribution for *Celdobolus* sp., *Babinka prima* Barrande, 1881 and *Wosekella* sp. at all sites. **B)** Shapiro-Wilk p-values for normality. **C)** t-test p-values for significant differences in size between sites.

FIG. 4.—Model explaining the influence of storms on brachiopod and bivalve communities in the lower part of the Fezouata Shale (upper Tremadocian), Zagora area (Morocco).

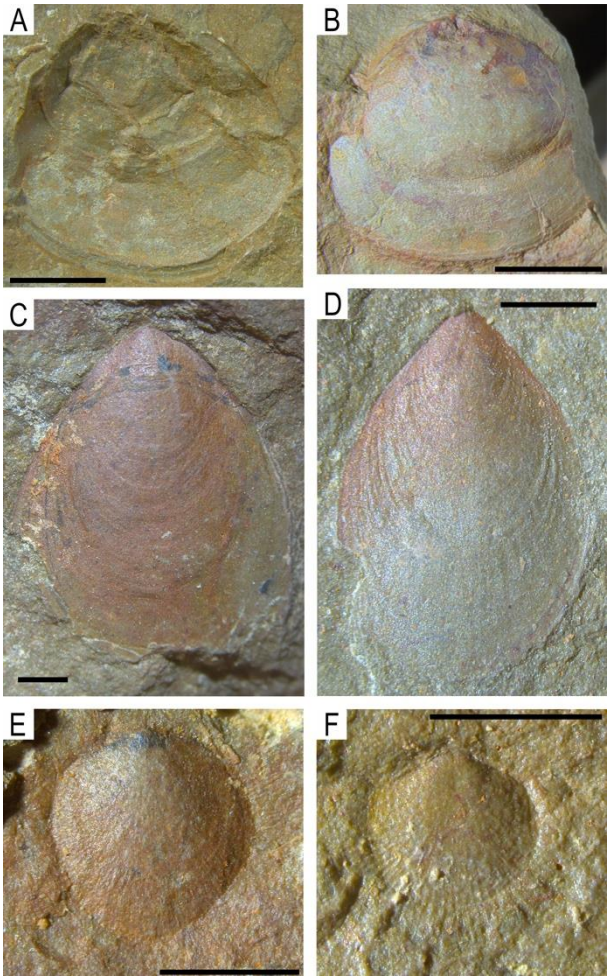

A
Formation
Age
Graptolite biozones
Synthetic log
Zini
FEZOUATA SHALE
FLOIAN
TREMADOCIAN
CAMBRIAN
UPPER
MIDDLE
LOWER
'Azygograptus interval'
?
Schizograptus sp.
Baltograptus minutus
?Baltograptus jacksoni
?Cymatograptus protobalticus
Hunnegraptus copiosus
Araneograptus murrayi
Aorograptus victoriae
Rhabdinopora flabelliformis anglica
Anisograptus matanensis
850
800
750
700
650
600
550
500
450
400
350
300
250
200
150
100
50
10
KsL
Upper interval
KsL
Lower interval (studied localities)


B
sediments
Rare cm-scale HCS
Stacking of storm events
Coarse sediments
Decimetric-scale HCS
Z-F2(1,2)
Z-F4
Z-F3
Z-F2(3)
Z-F51
Z-F50
Distal
Proximal


C
Z-F2(3)
Z-F4
Z-F2(1,2)
Z-F3
Zagora
Z-F51
Z-F50
Google Earth


D
Zagora
Morocco
Océan Iapetus
Baltica
Avalonia
Océan Rhéique
30°
60°
90° S
Gondwana

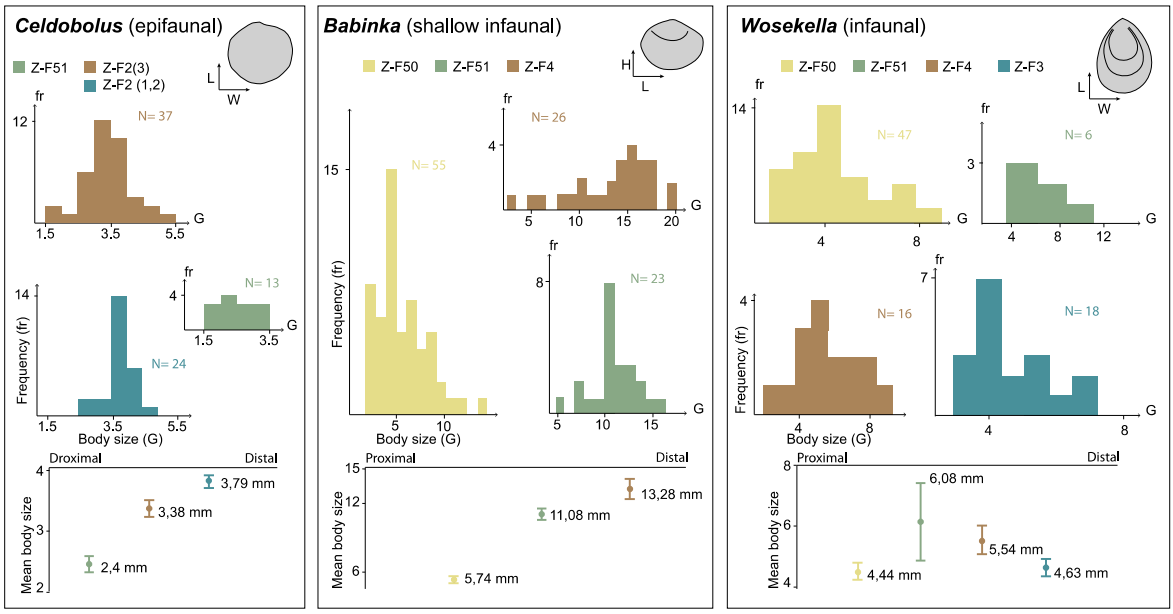
500



501

502

A



B

Shapiro Wilk	Z-F51	Z-F2(3)	Z-F2(1,2)
p	0,47	0,18	0,27

Shapiro Wilk	Z-F50	Z-F51	Z-F4
p	0,054	0,84	0,083

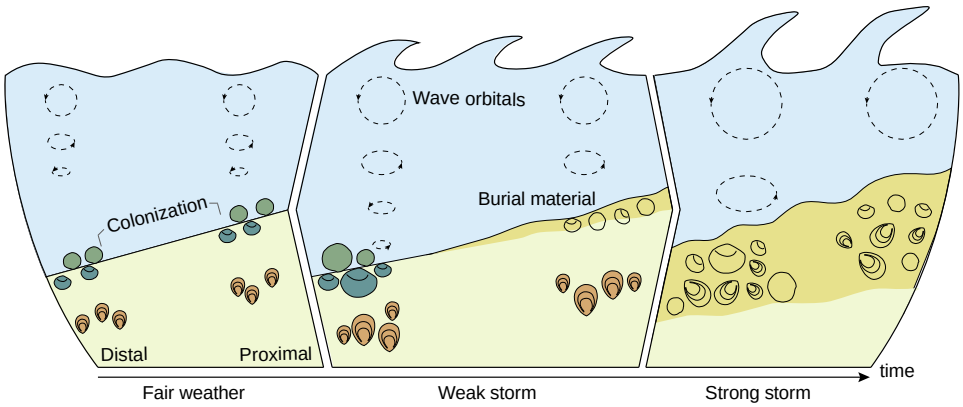
Shapiro Wilk	Z-F50	Z-F51	Z-F4	Z-F3
p	0,062	0,21	0,87	0,137

C

p (t-test)	Z-F51	Z-F2(3)	Z-F2(1,2)
Z-F51		0,0017	$9{,}45.10^{-10}$
Z-F2(1-2)			0,031
Z-F2(3)			

p (t-test)	Z-F50	Z-F51	Z-F4
Z-F50		$1{,}64.10^{-14}$	$8{,}25.10^{-16}$
Z-F51			0,033
Z-F4			

p (t-test)	Z-F50	Z-F51	Z-F4	Z-F3
Z-F50		0,06	0,054	0,62
Z-F51			0,69	0,1
Z-F4				0,09
Z-F3				


Wave orbitals
Colonization
Burial material
Distal
Proximal
time
Fair weather
Weak storm
Strong storm

505